Open-top CO_2-enrichment chambers in a field of cotton at Phoenix, Arizona, USA. They were used to obtain some of the cotton yield response data in Figure 2. Photo taken by Bruce A. Kimball, USDA, Agricultural Research Service, US Water Conservation Laboratory on 9 June 1987.

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Effects of increasing atmospheric CO_2 on vegetation

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Abstract

The increasing atmospheric CO_2 concentration probably will have significant direct effects on vegetation whether predicted changes in climate occur or not. Averaging over many prior greenhouse and growth chamber studies, plant growth and yield have typically increased more than 30% with a doubling of CO_2 concentration. Such a doubling also causes stomatal conductance to decrease about 37%, which typically increases leaf temperatures more than 1 °C, and which may decrease evapotranspiration, although increases in leaf area counteract the latter effect. Interactions between CO_2 and climate variables also appear important. In one study the growth increase from near-doubled CO_2 ranged from minus 60% at 12 °C to 0% at 19 °C to plus 130% at 34 °C, suggesting that if the climate warms, the average growth response to doubled CO_2 could be consistently higher than the 30% mentioned above. Even when growing in nutrient-poor soil, the growth response to elevated CO_2 has been large, in contrast to nutrient solution studies which showed little response. Several studies have suggested that under water-stress, the CO_2 growth stimulation is as large or larger than under wellwatered conditions. Therefore, the direct CO_2 effect will compensate somewhat, if not completely, for a hotter drier climate. And if any climate change is small, then plant growth and crop yields will probably be significantly higher in the future high-CO_2 world.

Introduction

The CO_2 concentration of the atmosphere is increasing, and climate modelers have predicted a consequent global warming and changes in precipitation patterns. The report of the Intergovernmental Panel on Climate Change edited by Houghton *et al.* (1990) projects CO_2 increasing from present day concentrations of about 350 μL/L[1]* to over 800 μL/L by the end of the next century if no steps are taken to limit emissions. They predict this increase in CO_2 plus that of other radiatively active 'greenhouse' gases – methane, nitrous oxide, chlorofluorocarbons (CFC's), ozone – would cause an increase in global mean temperature of about 4.2 °C. Some regions probably will receive increases in precipitation, whereas others will receive less, but these changes are very uncertain.

This increase in CO_2 and possible concomitant climate change could affect the ecology of most living things, including production agriculture. However, the increasing CO_2 concentration also will directly affect growth of all plants whether the climate changes or not. The main purpose of this paper is to describe these direct effects of increased CO_2 on plants and also to discuss some interactions between CO_2 and climate variables that are likely to have important consequences for

* 1 μL/L = 1 microliter CO_2 per liter of air = 1 ppmv = 1 part per million by volume = 1 μmol/mol

the growth of vegetation in the future high-CO_2 world.

History of research about CO_2 and plants

The first recorded observation of the effect of CO_2 on plant growth is attributed to de Sassure in 1804, who noted that pea plants grew faster when exposed to an atmosphere enriched with CO_2. Since that time, numerous experiments have documented that plants generally exhibit faster growth when the CO_2 around their leaves is increased. Table 1 adapted from Wittwer (1986) lists milestones in research into the effects of CO_2 on plants and its ultimate exploitation by CO_2 enrichment of greenhouses. By 1961, there were 4000 acres of greenhouse crops being grown with CO_2 enrichment in the Netherlands. Today it is a standard recommended horticultural practice for growers to enrich their greenhouses to about 1000 $\mu L/L$ of CO_2 whenever possible (i.e. when the greenhouses are not being ventilated for temperature control). Thus, the projected CO_2 concentration of the global atmosphere of the future is similar to that being deliberately created by today's greenhouse growers.

Table 1. Milestones in CO_2 enrichment of greenhouses. Adapted from Wittwer (1986).

Year	Observations	Observer
1648	Major increase in mass of a willow came from the atmosphere	Van Helmont
1804	First observations of CO_2 enhancement of plant growth	de Sassure
1902	Negative effects of CO_2 enhancement on plant growth	Brown & Escombe
1902–1894	Positive effects of CO_2 enhancement on plant growth (Europe)	Demoussy
1918	Positive effects of CO_2 enhancement on plant growth (U.S.A.)	Cummings & Jones
1931	6,000 nurseries reported using CO_2 in Germany	Reinau
1959	Basic studies on CO_2 and light responses in plants	Gaastra
1961	Dutch growers add CO_2 for improving yields of 4,000 acres of lettuce	Anon.
1962	Response of cucumber reported and the complimentary effects of CO_2 and light	Hopen & Ries; Daunicht
1962–1966	Responses of flower crops reported	Goldsberry & Holley
1964	Comprehensive studies on tomato and cucumber	Wittwer and Robb
1976	Positive effects noted for the growth of tree seedlings	Hannover *et al.*

Photosynthesis

According to Table 1 from Wittwer (1986), the effect of varying CO_2 concentration on photosynthesis was firmly established about 1959 by Gaastra. Recalling the overall process of photosynthesis, CO_2 and water are combined in plant leaves utilizing sunlight to produce carbohydrates and oxygen.

$$CO_2 + H_2O \xrightarrow{\text{light}} CH_2O\ (\text{carbohydrate}) + O_2$$

From carbohydrates, plants make proteins, lipids, and other biological substances that form their bodies. And then they are eaten by herbivores, which are eaten by carnivores and so on up the food chain. Thus, although CO_2 may be regarded as a problem at the present time, one can see that it really should not be regarded as a pollutant; rather, it is really one of the feedstocks which make life itself.

The chemical equation above ignores numerous intermediate steps and compounds in the photosynthetic process, some of which are important in determining how a plant will respond to increasing CO_2. Figure 1 adapted from Taiz & Zeiger (1991) shows how net photosynthesis changes with CO_2 concentration for two groups of plants: C_3 and C_4. The C_3 plants are so-called

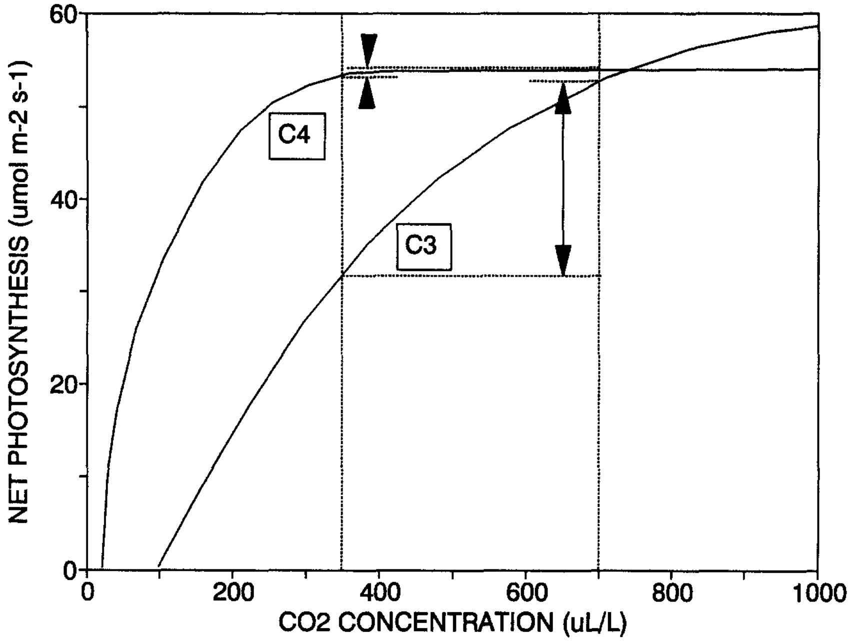

Fig. 1. Net photosynthesis of typical C_3 and C_4 plants versus CO_2 concentration, adapted from Taiz and Zeiger (1991). The vertical dotted lines at 350 and 700 μL/L indicate the present-day CO_2 concentration and the doubled concentration projected to occur sometime near the end of the next century (Houghton *et al.* 1990), respectively. The double arrows indicate the amounts of increase in photosynthesis due to the CO_2 doubling.

because one of the first intermediate compounds, phosphoglyceric acid, has 3 carbon atoms, and in like manner the C_4 plants have a 4 carbon compound, oxaloacetic acid. Most agricultural crops, including wheat, rice, barley, oats, soybeans, potatoes, cotton, tree crops, etc. belong to the C_3 group. The C_4 plants include tropical grasses of which corn, sorghum, sugarcane, and millet are the most important crops.

Referring to Fig. 1, at a present day CO_2 concentration of 350 μL/L, the C_4's have a higher photosynthetic rate, consistent with the fact that C_4 corn growth and yields are generally greater than those of C_3 wheat. However, as CO_2 concentration is increased to say 700 μL/L, the rate of the C_3 group increases about 66%, which is *relatively* much more than the small increase of about 4% for the C_4's. Therefore, we can expect that yields of C_3 wheat will increase relatively more than those of C_4 corn and that yields of C_3 sugarbeets will increase relatively more than those of C_4 sugarcane as the atmospheric CO_2 concentration increases. With relative changes in productivity, there will be relative changes in profitability and subsequent changes in portions of land area devoted to various crops.

Furthermore, the differing responses to CO_2 between C_3 and C_4 species are likely to change their competitiveness. As reviewed by Patterson & Flint (1990), C_3 weeds are likely to become more of a problem in C_4 crops, while C_3 crops should gain some advantage over C_4 weeds. Similarly, in natural vegetation C_3 species are likely to gain advantage over C_4 species, which could markedly change the complexion of some ecosystems.

Growth and yield

Figure 1 shows how photosynthesis is increased by an increase in atmospheric CO_2 concentration. Of crucial importance is whether the actual growth of plants will be similarly increased, because there are numerous intermediate steps before the carbohydrates produced in the leaves are transformed into root, stem, flower, fruit, seed, or additional leaf tissue. For the most part, the answer appears to be 'yes, growth and yield are also increased'. At the USDA-ARS U.S. Water Conservation and the Western Cotton Research Laboratories we have conducted CO_2 enrichment experiments on field-grown cotton using open-top CO_2-enrichment chambers for several years (Kimball *et al.* 1983-1987, 1992). The seed cotton (lint + seed) yields from these experiments are presented in Fig. 2 versus CO_2 concentration. In spite of the year to year variability and the influence of other treatments, CO_2 obviously stimulated cotton yields, amounting to a 64% increase at 650 μL/L averaging over all the data.

Thus, cotton is highly responsive to additional

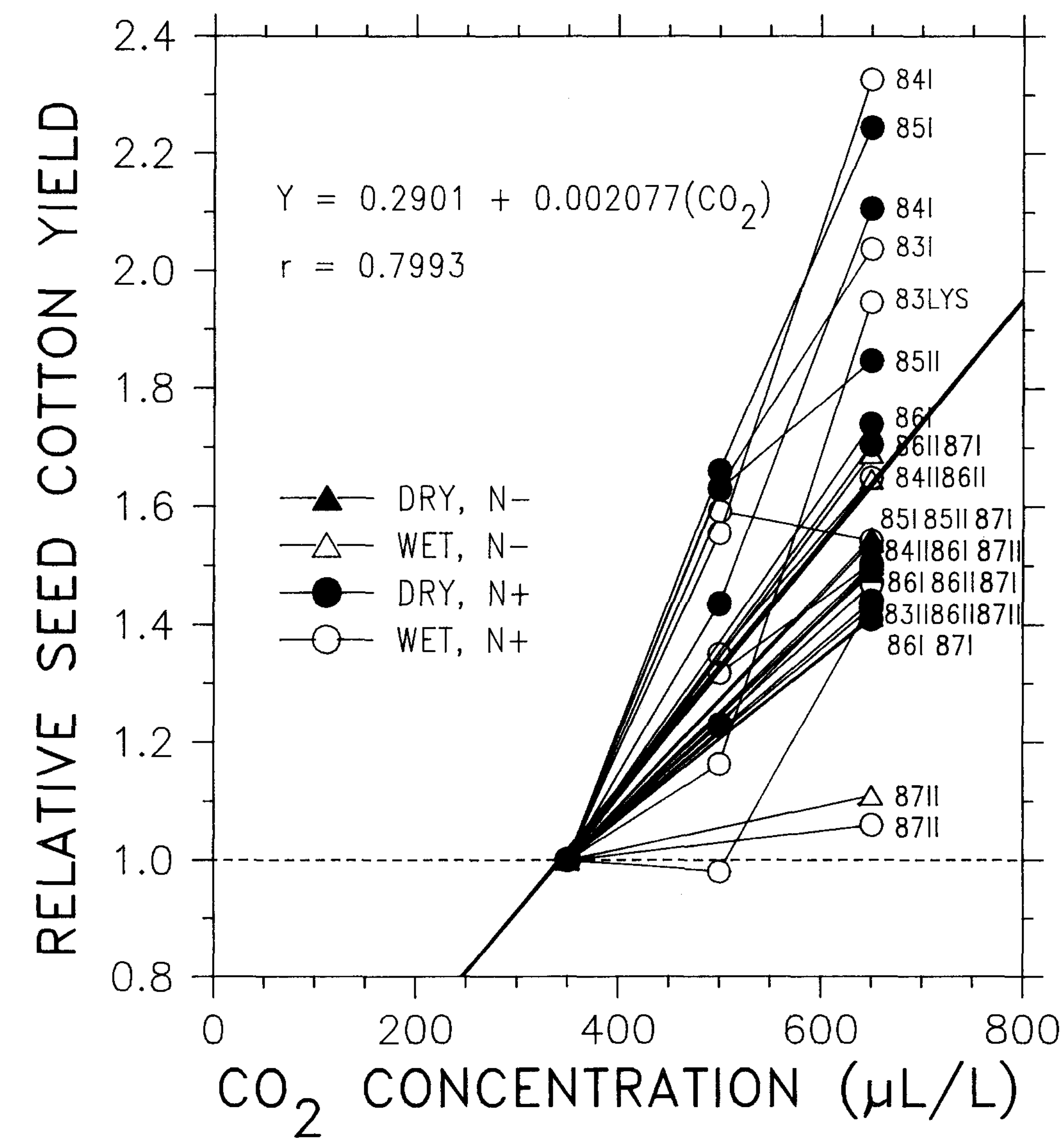

Fig. 2. Seed cotton yield (lint and seed) relative to the yield obtained from ambient CO_2 control chambers versus CO_2 concentration for 5 years' worth of experiments with open-top chambers at Phoenix, AZ. The labels on the right identify the year and replicate of the particular data points. From Kimball *et al.* (1987).

CO_2, but what about other species of vegetation? Kimball (1983) assembled and analyzed much of the existing data available from the literature in 1983 about the yield or growth response of 37 species of plants to CO_2, amounting to 430 prior observations. The average response was a yield increase of about 33%. Kimball (1986b) tabulated the percentage increases in yield to be expected with a doubling of CO_2 concentration to 660 μL/L for various classes of crops based on the prior CO_2 enrichment experiments. The increases amounted to 31, 31, 25, and 31% for C_3 fruit, grain, leaf, and legume seed crops, respectively. Non-agricultural C_3 herbaceous and woody species responded similarly with average growth increases of 34 and 26%, respectively.

Cure (1985) assembled the available data about the carbon exchange rate (net photosynthesis), biomass accumulation, yield, and other physiological parameters of 10 major crops – wheat, barley, rice, corn, sorghum, soybean, alfalfa, cotton, potato, and sweet potato. For C_3 cases where the number of studies was 10 or more (wheat, barley, rice, and soybean), the results of her analysis were close to the 33% reported by Kimball (1983, 1986b).

In a recent review, Allen (1991) tabulated the response of C_3 soybean to elevated CO_2. He concluded that a doubling of CO_2 concentration causes photosynthesis to increase about 50%, biomass accumulation to increase about 40%, and marketable seed yields to increase about 30%. He also states that the increase in CO_2 concentration from preindustrial levels (about 270 μL/L) to today's levels already should have increased soybean yields by 12%.

However, photosynthesis of C_4 species such as corn responds relatively less to an increase in CO_2 (Fig. 1), as discussed previously, so growth of C_4 species would also be expected to increase relatively less than those of C_3 species. Kimball (1986b) found only 13 C_4 growth observations, but which had an average yield or growth increase of about 14% with a doubling of CO_2. The analysis by Cure (1985) showed biomass accumulations for corn and sorghum of 9%. These growth data are consistent with the photosynthesis differences, but the amount of data on C_4 species is too sparse to draw many firm conclusions.

Stomatal conductance

Carbon dioxide has another important direct effect on plants that affects their water relations. Increasing the CO_2 concentration in the atmosphere around a leaf causes the stomates to partially close, which reduces the transpiration or rate of loss of water from the leaf. Stomatal conductance is a parameter that characterizes the ability of the stomates to transmit water vapor from inside the leaf to the air surrounding the leaf. Morison (1987) analyzed data from the literature and showed that a doubling of CO_2 concentration to 660 μL/L reduced stomatal conductance to 60% of that at 330 μL/L. He also showed that there is no significant difference between the C_3 and C_4 groups of plants in their stomatal conductance response to increasing CO_2. Thus, C_4 corn should derive as much drought tolerance as C_3 wheat, even though the corn's photosynthetic rate is not expected to increase as much as that of wheat.

The partial closing of the stomates with a doubling of CO_2 has several consequences, which may or may not be important depending on circumstances. One immediate effect is a reduction of transpirational cooling of the leaves. We (Idso *et al.* 1987a) have measured the temperatures of cotton canopies using noncontact infrared thermometers, and we have found that in general the temperature of a cotton crop with ample water is increased about 1 °C (2 °F) by a doubling of CO_2 concentration to about 650 μL/L. The stomates of cotton seem to respond less to CO_2 than do those of most other crops, so the temperature rise of most other crops may be even greater. Such increases in foliage temperature are probably good if present temperatures are below the optimum for the crop, but could be harmful if present temperatures are above the optimum – just as the projected climate warming may benefit or harm a particular plant depending on where temperatures presently are with respect to its optimum.

Another consequence of the partial stomatal closing could be a significant reduction in evapotranspiration, ET, or rate of water loss per unit of land area by a crop (transpiration from the leaves plus evaporation from the soil surface). Rosenberg *et al.* (1990) recently used a simple but theoretically robust equation (Penman-Monteith) to calculate the effect of increasing CO_2 and climate change on closed canopies of wheat and two other ecosystems. Table 2 shows a portion of their work for a wheat crop at Mead, Nebraska. The predicted climate change scenarios for Mead from three general circulation models are presented, and perhaps the most striking aspect of Table 2 is the large difference among the general circulation models' (GCMs') predicted climate changes for that particular spot on the globe. [In spite of this large range in regional predicted temperature change from -1.1 to $+6.3$ °C (-2.0 to $+11.3$ °F), the models have much closer agreement in their global average predicted change.] Focussing on the GISS data (which are closest to the predicted global changes), a temperature increase of 3.6 °C alone is predicted to increase ET by 24%. When additional predicted changes in radiation, vapor pressure, wind speed were accounted for, ET was predicted to increase 9%. Further accounting for the decrease in stomatal conductance (or increase in resistance, r_s, in the notation of Rosenberg *et al.*) and for increased leaf area, LAI, with a doubling of CO_2 predicted only a 2% increase in ET. In other words, the decreased ET due to the direct effects of CO_2 on plants almost exactly compensated for the increased ET from the GISS climate change scenario.

Further discussion of Table 2 is needed because it presents only a one-time 'snapshot' of a wheat crop at midseason with complete canopy cover when directbeam sunlight rarely strikes the soil surface. Earlier in the season, crops growing at high CO_2 might have much larger leaf areas and therefore higher ET. Also, earlier in the season much of the water loss is evaporation from the soil, which would not be directly affected by changes in stomatal conductance. Therefore, if ET is integrated over an entire growing season, the total crop water requirement might be less

Table 2. Impact of climate changes on evapotranspiration, ET, predicted using the Penman-Montieth equation for scenarios of future climate predicted by general circulation models of the Goddard Institute for Space Studies (GISS), the Geophysical Fluid Dynamics Laboratory (GFDL), and the National Center for Atmospheric Research (NCAR) with and without expected changes in leaf area index, LAI, and canopy resistance r_s for a wheat field in Mead, Nebraska, in summer. Control is ET with no change from present climate. Adapted from Rosenberg *et al.* (1990).

GCM	Amount of change						ET (mm/hr)	Change in ET (%)
	Temperature (°C)	Radiation (%)	Vapor pressure (%)	Wind speed (%)	r_s (%)	LAI (%)		
Control							0.62	
GISS	3.6	–	–	–	–	–	0.77	24
	3.6	0	30	26	–	–	0.68	9
	3.6	0	30	26	40	15	0.63	2
GFDL	6.3	–	–	–	–	–	0.88	42
	6.3	14	24	−36	–	–	0.80	28
	6.3	14	24	−36	40	15	0.76	23
NCAR	−1.1	–	–	–	–	–	0.58	−7
	−1.1	0	22	100	–	–	0.48	−23
	−1.1	0	22	100	40	15	0.43	−30

affected by CO_2 than suggested by the calculations of Rosenberg *et al.* (1990). On the other hand, in areas covered with natural vegetation or with pasture or rangeland, a full canopy exits for a greater portion of the season than for cultivated crops. Therefore, for these areas ET may be affected more by CO_2 in accordance with the calculations of Rosenberg *et al.* (1990).

We (Kimball *et al.* 1983, 1984) attempted to measure the seasonal water use (predominantly evapotranspiration) for well-watered, field-grown cotton in open-top CO_2-enrichment chambers, but the results were not very consistent (Table 3). The most reliable data are from lysimeters which showed a slight overall decrease in water use at the elevated CO_2 concentrations. Even if water use changed little with CO_2 enrichment, nevertheless, there was a large increase in water use efficiency commensurate with the large increase in yield (Fig. 2).

Interactions among CO_2, climate variables, and soil fertility

Most of the preceding discussion dealt with the direct effects of CO_2 on plants without an accompanying change in climate. The prediction of an average yield increase of about 30% with a doubling of CO_2 for C_3 plants is based on studies with mostly optimum conditions of temperature, water, and soil nutrients. In this section we address how plant growth responses to CO_2 are affected by changes in these other variables (cf. Rozema, this volume).

We (Idso *et al.* 1987b) grew carrot, radish, water hyacinth, and azolla (water fern) year-around in open-top CO_2-enrichment chambers in Phoenix, Arizona. We similarly grew cotton in spring and summer. Weekly measurements of growth were made, as well as of mean daily air temperature which ranged from about 12 to 34 °C. Figure 3 is an aggregation of the data from all 5 species with 'growth modification factor', the increase in growth due to a near-doubling of CO_2 concentration, plotted against the mean daily air temperature for the two weeks prior to harvesting. There is much scatter in the data, but the growth modification factor appears to increase strongly with increasing temperature ranging from about −0.4 at 12 °C to 1.0 at 19 °C to 2.3 at 34 °C. We do not know why the plants would be harmed by high CO_2 at the lower temperatures, and other data suggest that the low temperature response may vary greatly among species. Another general observation is that the temperature optimum for photosynthesis shifts to higher temperatures with increasing CO_2 (Allen *et al.* 1990; Allen *et al.* 1991); based on this and other evidence, we believe that the greater CO_2 growth stimulation at higher temperatures is real.

If global temperatures increase as predicted, plants will be helped or harmed depending upon whether they are presently growing at temperatures below or above their optimum, as already mentioned. However, if temperatures do increase 3 °C as predicted for a CO_2 doubling, the regression in Fig. 3 suggests that the CO_2 growth stimulation may be closer to 56%, rather than the

Table 3. Total seasonal water use (evapotranspiration) for well-watered cotton versus CO_2 concentration in open-top CO_2-enrichment chambers. The numbers in parenthesis are the percentage change from ambient. Adapted from Kimball *et al.* (1983, 1984).

Year	Rep	Method	CO_2 concentration (μL/L)		
			Ambient	500	650
			(mm)		
1983	I	Lysimeters	1100	1000 (−9)	1052 (−4)
1083	II	Neutron probe	780	770 (−1)	810 (+4)
1984	I	Neutron probe	570	670 (+18)	730 (+28)
1984	II	Neutron probe	750	710 (−5)	770 (+3)

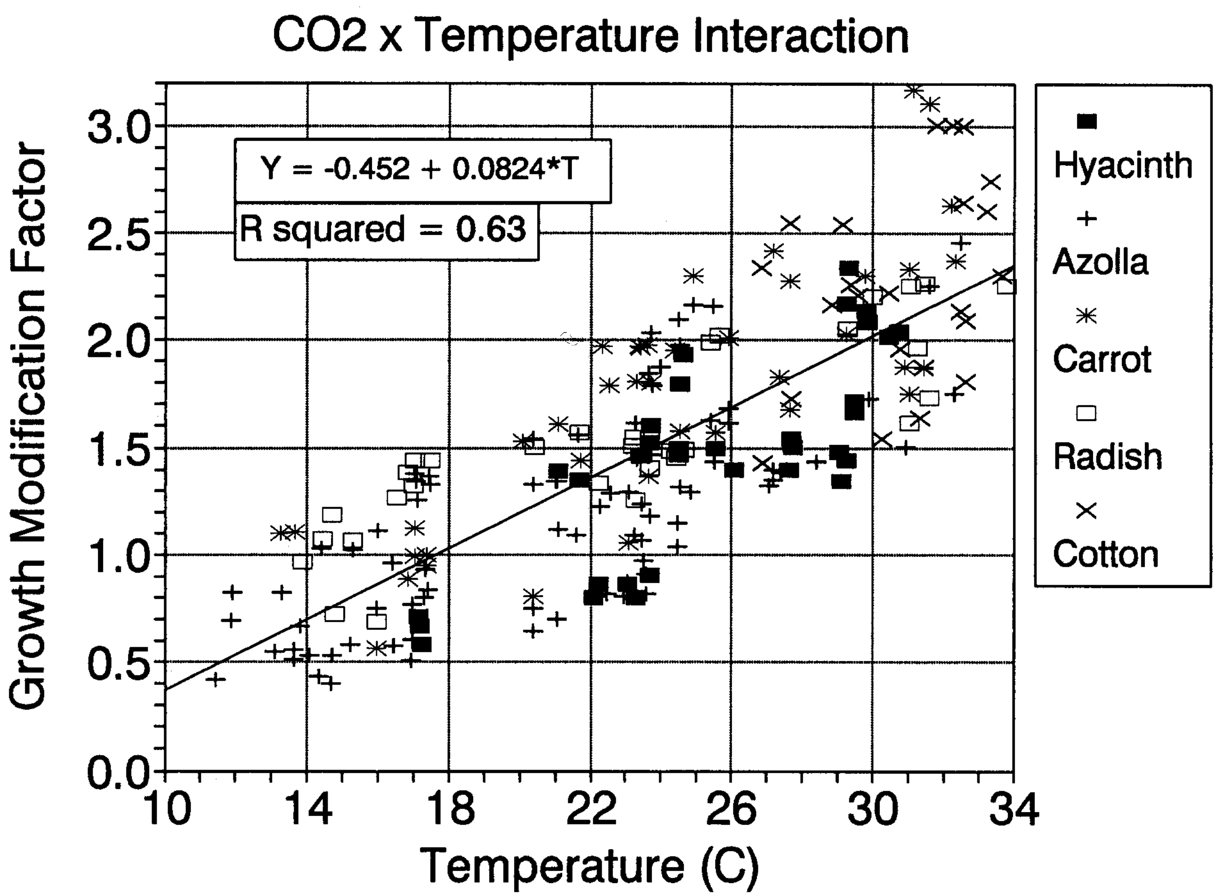

Fig. 3. Plant growth modification factor (or relative increase in growth) due to a 300 $\mu L/L$ increase in CO_2 concentration (a near doubling) versus mean air temperature. The data are for water hyacinth, azolla (water fern), carrot, radish, and cotton. Adapted from Idso *et al.* (1987b).

mean 32% presented earlier. Therefore, a present-day cool climate like that of Canada, Northern Europe, or the Soviet Union conceivably could get a triple benefit from the predicted CO_2 increase and global warming (if precipitation is adequate). (1) The increase in air temperature raises crop temperature closer to optimum and growing seasons may be longer. (2) The crop grows faster because of the stimulation due to CO_2. (3) And it grows faster yet because of the interaction between CO_2 and temperature.

But the yields of some crop species growing in cool climates might be decreased by a temperature increase. Goudriaan & Unsworth (1990) for example describe how *determinate* crops with a discrete life cycle such as wheat may mature faster, thereby shortening their growing season even while the frost-free period may be getting longer. With elevated CO_2 they should experience some yield increase, nevertheless.

Figure 3 also suggests that crops growing at cooler temperatures will be stimulated relatively less by elevated CO_2. Therefore, if the climate does not warm as predicted, then the growth of crops in cooler climates will be stimulated relatively less from the increased CO_2 than those of warmer regions.

The drought in midwestern United States during the summer of 1988 raised the concern of many people that climate change might be a real possibility and that it might have severe consequences for agriculture. For that reason, the effects of CO_2 on plant growth when water is in short supply are of great interest and importance. We (Kimball *et al.* 1984-1987, 1992) conducted a series of experiments with cotton growing in open-top CO_2 enrichment chambers that included a well-watered ('wet') treatment and also a water-stress ('dry') treatment that received 2/3 as much water as the wet treatment. The results of these experiments are summarized in Table 4, which shows that under conditions of water-stress (and added nitrogen), a near-doubling of CO_2 increased seed cotton yields an average 74%, compared to 56% under well-watered conditions. The 1984 year was the one exception in which the wet response to CO_2 was greater than in the dry. That year untimely rains and a poorly designed flood irrigation system prevented good control of the water stress treatment, so the 1984 data should be given less weight. Thus, these data show that even under conditions of water stress, a doubling of CO_2 produces large stimulations in plant growth.

Similar results showing large growth responses to elevated CO_2 even under water stress conditions have been observed with wheat and other crops (Kimball 1985). Whether the beneficial effect of CO_2 is adequate to compensate fully for a climatic change to drier conditions, however, depends much on the severity of the future droughts, which is a very uncertain prediction from the climate models. The photosynthesis equation presented earlier has carbohydrate as the primary product, and Fig. 1 shows how its rate increases with increasing CO_2. However, plants also need nitrogen, N, (and other nutrients) in order to make protein from the carbohydrate and grow. If they cannot get the needed N because of low soil fertility or other reasons, the concept of limiting factors says that an increase in CO_2 will not make them grow faster. Although there was much scatter, a review by Kimball (1986a) indicated a lower response to CO_2 enrichment at the lowest N concentrations in several non-soil nutrient solution experiments.

Table 4. Percentage increase in seed cotton yield due to a near-doubling of CO_2 under well-watered (wet) and water-stressed (dry) treatments and under low (no added N) and more normal (added nitrogen) levels of nitrogen fertilizer for 5 years of experiments with open-topped chambers at Phoenix, AZ. Adapted from Kimball *et al.* (1987).

Year	Added nitrogen		No added N	
	Wet	Dry	Wet	Dry
	(%)			
83	63	–	–	–
84	94	77	–	–
85	52	104	–	–
86	48	70	70	51
87	25	43	37	52
Ave.	56	74	54	52

In contrast to the nutrient solution experiments, Table 4 shows the results from 2 seasons for cotton growing in soil when there was a 'no added nitrogen' treatment (Kimball *et al.* 1986–1987, 1992). This low nitrogen 'stress' was severe enough to depress yields, but under both wet and dry conditions there was about a 53% increase in seed cotton yield due to a near-doubling of CO_2. These results with plants growing in soil conflict somewhat with the nutrient solution experiments discussed previously, and they suggest that with CO_2 enrichment, plants are capable of getting more nitrogen from nitrogen-poor soil, and that if low fertility does limit the response to CO_2 of plants growing in soil, the fertility level must be very low indeed. Therefore, the beneficial effects of elevated CO_2 may well extend to vegetation that is growing without added fertilizer, which is of particular importance to third world countries and to natural unmanaged ecosystems.

Conclusions

Based on the work presented, the following conclusions can be drawn about the effects of an elevated CO_2 concentration on vegetation.

1. In the absence of climate change, a doubling of atmospheric CO_2 concentration will probably increase plant growth and yields by an average of about 30%.
2. Plants vary in the degree of their response to

CO_2, especially C_3 respond more than C_4 photosynthetic types. The differences in response likely will affect proportions of land area divided among the various crops in the future. The differing responses to CO_2 will likely also affect competition among species.
3. There appears to be a strong positive interaction between CO_2 concentration and temperature, which could greatly increase the CO_2 growth stimulation under some conditions, but decrease it under other conditions.
4. Stomatal conductance will probably be reduced at higher CO_2 concentrations which will reduce transpiration per unit of leaf area and consequently increase leaf temperatures. But with increased leaf area, seasonal water use per unit of land area may be minimally affected.
5. The growth response to elevated CO_2 is large, even under water-stress conditions.
6. Plants growing in nutrient-poor soil also respond to elevated CO_2, although the response may be reduced under very severe nutrient deficiencies.

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